VEGETATION AND VASCULAR FLORA OF TALLGRASS PRAIRIE AND WETLANDS, BLACK SQUIRREL CREEK DRAINAGE, SOUTH-CENTRAL COLORADO: PERSPECTIVES FROM THE 1940s AND 2011

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ABSTRACT

We examined a tallgrass prairie-wetland complex of the Black Squirrel Creek drainage in south-central Colorado to compare the current grassland composition to its documentation by Robert Livingston in the early 1940s. Livingston considered these grasslands as probable Pleistocene relicts analogous to Midwestern tallgrass prairie with respect to dominant grasses and forbs. Using Livingston's methodology, we assessed an area near his original plots to determine whether the dominant grass species had changed in their contributions to cover or frequency. We found an almost identical suite of species to those documented in the 1940s, with modest differences in frequency and relative contribution to cover by the key grasses. We also characterized wetland habitats occurring within the grassland matrix, documented the vascular flora of mesic and hydric habitats, and analyzed the extent to which they contain species of conservation concern, Midwest prairie elements, or montane species typically occurring regionally at higher elevations. The tallgrass communities here differ from others in Colorado and the Midwest in having a lower abundance of *Andropogon gerardii,* and being dominated by *Sporobolus heterolepis* along with xeric species like *Bouteloua gracilis* and *Calamovilfa longifolia*, and montane species like *Muhlenbergia montana.* Although the structure of the extant vegetation remains similar to what existed in the 1940s and continues to be supported by ample groundwater, these grasslands are now reduced in extent. The vegetation mosaic of tallgrass prairie and wetlands holds a rich flora with numerous elements of phytogeographic and conservation interest.

RESUMEN

Examinamos el complejo de praderas de hierbas altas y humedales del desagüe de Black Squirrel Creek, en el sur-centro de Colorado, para comparar la composición actual de las praderas con la que Robert Livingston documentó a principios de los años cuarenta. Livingston consideró que estas eran análogas a las praderas de hierbas altas del Medio Oeste, con respecto a los pastos y formas dominantes, probables relictos de la vegetación del Pleistoceno. Usando la metodología de Livingston, evaluamos un área cercana a las parcelas originales para determinar si las especies dominantes de pastos han cambiado en su contribución a la cobertura o en su frecuencia. Encontramos un conjunto de especies casi idéntico al de las documentadas en los cuarenta, con diferencias pequeñas en frecuencia y contribución a la cobertura por parte de pastos clave. También caracterizamos los humedales presentes en el marco de la pradera, documentamos las plantas vasculares de hábitats mésicos e hídricos, y analizamos en qué medida estos contienen especies de interés para la conservación, elementos de las praderas del Medio Oeste o especies montanas comunes en regiones de mayor altitud. Las comunidades de pastos altos en este lugar difieren de otras en Colorado y en el Medio Oeste por la menor presencia de *Andropogon gerardii* y la presencia dominante de *Sporobolus heterolepis,* junto con especies áridas o montanas, como *Bouteloua gracilis, Calamovilfa longifolia* y *Muhlenbergia montana.* Aunque la estructura de la vegetación existente sigue siendo similar a la de los años cuarenta y aún cuenta con el soporte de abundantes aguas subterráneas, la extensión de estas praderas se ha reducido. El mosaico de vegetación de praderas de hierbas altas y humedales conserva una rica flora con numerosos elementos de interés para la geobotánica y la conservación.

INTRODUCTION

Over the past century, Colorado prairies changed and diminished as urban, suburban, and exurban development expanded while fire suppression, invasion of exotic species, and overgrazing altered grassland compo-

nents. Prairie vegetation overall, and tallgrass communities in particular, now elicits special conservation focus amid widespread concerns about accelerating loss, fragmentation, and degradation throughout the Midwest and West (Nicholson & Hulett 1969; Samson & Knopf 1996; Bachand 2001; Colorado Natural Heritage Program 2005; Rondeau et al. 2011). In the early 1940s, ecologist Robert Livingston undertook a detailed study of tallgrass prairie in south-central Colorado north of Colorado Springs (Fig. 1). He profiled this vegetation in his graduate theses and related publication (1941, 1947, 1949, 1952) as unique remnant vegetation with strong floristic similarities to the Midwest prairies. This work provided a portrait of regionally anomalous vegetation as it existed nearly seventy years ago.

In this study, we reanalyzed the grassland vegetation in the Black Squirrel Creek drainage (Fig. 2) that was the focus of Livingston's work. We compared its current composition to the earlier descriptions and added additional documentation of associated wetland communities and the vascular flora. Although these additional components were not a focus in the original Livingston studies, contemporary conservation interest in these elements suggested their importance as part of the regional ecological profile. The objectives of our study were to:

1) Document the flora of the mesic and hydric communities and assess the extent to which this flora contains elements from the Midwest prairie or other regional components such as montane species typically occurring in the foothills, and highlight species of concern.
2) Document the types of wetland habitats occurring in the grassland matrix and their signature flora, plant associations and hydrogeomorphic profiles.
3) Compare the current dominant species and composition of the vegetation to the 1940's profile considered representative of Midwestern tallgrass prairie. In particular, we examined whether the relative rank of the dominant grass species had changed with respect to contribution to cover and frequency.

Regional vegetation contexts: shortgrass, mixed grass and tallgrass prairie

The eastern plains of Colorado encompass a wide range of grassland communities across diverse topography and edaphic substrates (Ramaley 1919; Shantz 1923; Weaver & Fitzpatrick 1934). These grasslands represent the western edge of the Great Plains, where collective vegetation types and many individual biotic components have been diminished from their historic presence (Rondeau et al. 2011). Shortgrass prairie (also known as shortgrass steppe senus Lauenroth et al. 2008) with its signature species *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths (nomenclature herein follows the U.S. Dept. of Agriculture National Resources Conservation Service Plants Database 2013 (www.plants.usda.gov); see Appendix 1 for full citations and exceptions) is the dominant regional vegetation (Weaver 1954; Neeley et al. 2006; Lauenroth et al. 2008). Shortgrass prairie south of Denver typically lacks extensive amounts of *Buchloe dactyloides*, a codominant elsewhere in shortgrass prairie, although it occurs sporadically in the shortgrass matrix here. In the piedmont east of the Colorado Front Range foothills, a mixed grass prairie prevails, where grama grass is present in conjunction with a high representation of species in *Elymus*, *Hesperostipa*, *Muhlenbergia,* and *Poa* along with *Schizachyrium scoparium* (Michx.) Nash), *Sporobolus cryptandrus* (Torrey) A. Gray, and *Koeleria macrantha* (Ledeb.) Schult. This vegetation is extensive north and east of Colorado Springs, where the topographic watershed known as the Palmer Divide separates the drainages of the South Platte River to the north and the Arkansas River to the south.

Limited occurrences of tallgrass prairie vegetation (Vestal 1914, 1917, 1919; Moir 1972; Bock & Bock 1998) exist just east of the Front Range in areas where edaphic conditions enhance soil moisture (Branson et al. 1965). The Colorado Natural Heritage Program (2012) tracks four tallgrass communities of conservation concern: xeric tallgrass prairie dominated by *Andropogon gerardii* Vitma and *Sporobolus heterolepis* (A. Gray) A. Gray), or *A. gerardii* and *Schizachyrium scoparium* (Michx.) Nash), and mesic tallgrass prairie dominated by *A. gerardii* and *Calamovilfa longifolia* (Hook.) Scribn.), or *A. gerardii* and *Sorghastrum nutans* (L.) Nash). These associations are part of mixed vegetation that comprises the collective Western Great Plains Foothill and Piedmont Grasslands (Colorado Natural Heritage Program 2005).

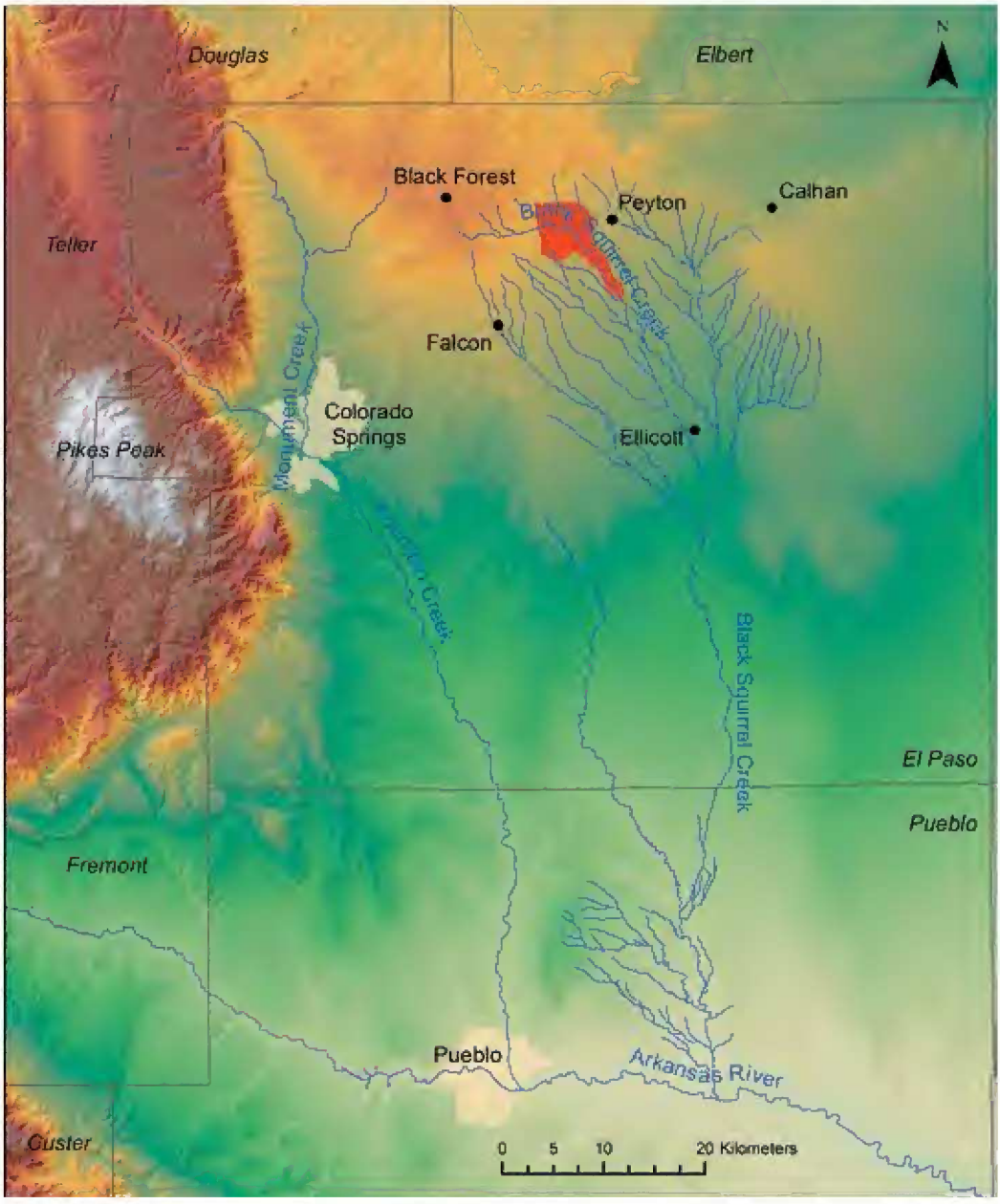

Fig. 1. Generalized area of study and Black Squirrel Creek drainage. Main study site is noted in red shading. The Palmer Divide is the region between El Paso and Douglas Counties, and represents the hydrological divide between the Platte and Arkansas Rivers.

At the species level, Colorado tallgrass prairies parallel those found in the Midwest where signature taxa include *Andropogon gerardii*, *Hesperostipa spartea* (Trin.) Barkworth), *Panicum virgatum* L., *Sorghastrum nutans*, and *Sporobolus heterolepis*, as well as the sand prairie tallgrass species *Calamovilfa longifolia* (e.g., Weaver 1954; Freeman 1998). The relative amounts of these species typically differ among central and western states (Weaver 1954; Weaver & Albertson 1956) according to precipitation and temperature regimes and soil types; in

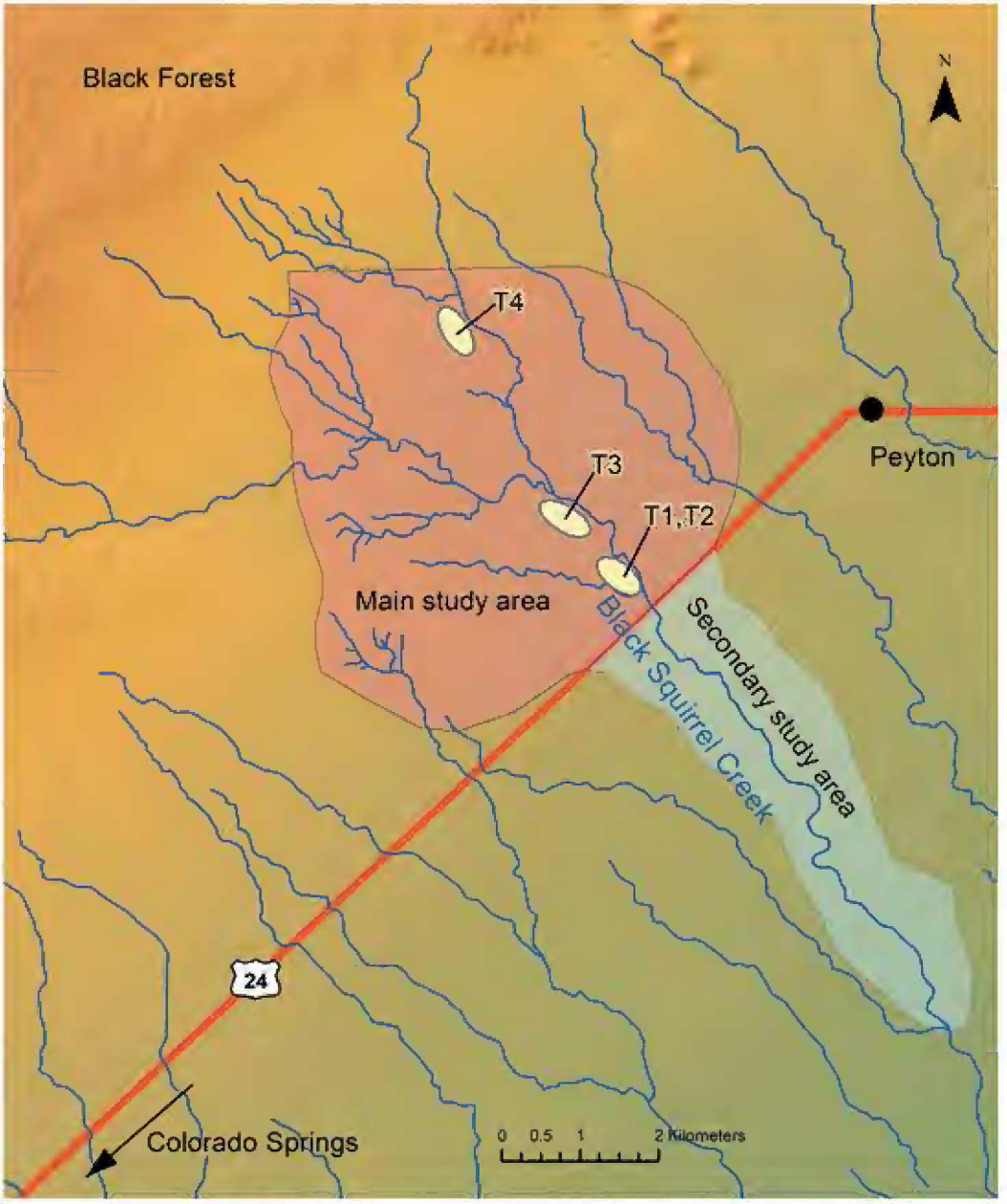

Fig. 2. Core study site along upper Black Squirrel Creek drainage, east of Colorado Springs. Transect locations are indicated by numbered ellipses; sizes are exaggerated for clarity.

Colorado, it has long been recognized that these communities similarly vary along a north-south gradient (Robbins 1910; Vestal 1914, 1917, 1919).

South of the Palmer Divide, isolated examples of tallgrass prairie occur within a ponderosa pine forest-grassland matrix known as the Black Forest (Shaddle 1939; Fig. 1). Studies by Vestal (1917), Shaddle (1939), and Williams and Holch (1946) noted the unusual vegetation and flora here. This region and surrounding

grasslands became the focus of studies in which Livingston (1941, 1947, 1949, 1952) highlighted the similarity of the grassland vegetation and flora to Midwestern "true prairie", and suggested it represented fragmented relict communities from the Pleistocene (Livingston 1952; Weaver and Albertson 1956). Although relatively recent studies of tallgrass vegetation in eastern Colorado have been conducted in the Boulder area ca. 150 km north of the Black Forest (e.g., Moir 1972; Baker & Galatowitch 1985; Bock & Bock 1998; Neid et al. 2009), no assessment of the Black Squirrel Creek vegetation has been done since those of Livingston, although surveys by the Colorado College Herbarium and the Colorado Natural Heritage Program (Doyle et al. 2001a; 2001b) have shown the area to be rich in rare species and ecological communities.

Study Site

The Black Squirrel Creek system, a complex anastomosed network of drainages into the main creek channel, begins near the summit of the Palmer Divide (Figs. 2, 3) in the Black Forest and extends southeast, ultimately draining into the Arkansas River east of the city of Pueblo. In the upper quarter of the drainage, the creek typically has perennial flow, but this becomes intermittent aboveground to the south. Our primary study area was located on the upper Black Squirrel drainage between the municipalities of Falcon and Peyton, with an elevation range of ca. 2000 to 2200 m (6500 to 7100 ft). Quantitative data were taken on the core area covering ca. 770 ha (1900 acres) on a ca. 3100 ha (7700 acre) ranch that encompasses the main stem of Black Squirrel Creek with perennial flowing water, as well as with subsidiary drainages with intermittent flow and standing water. We took additional floristic and qualitative information south of the core area for a distance of ca. 10 km in order to encompass the area utilized in the 1940's studies. The topography consists of gently rolling uplands of mixed grass prairie on Quaternary deposits of aeolian sand (Morgan & Barkmann 2012) separated by lowland drainages and swales with small discontinuous wetlands, seeps, springs, and seasonal ponds supported by groundwater. Our study focused on the mesic and hydric flora and vegetation occurring in these drainages, the associated wetlands, and streambeds of Black Squirrel Creek and its tributaries rather than the xeric and mixed grass vegetation of the uplands that is widely represented on the plains.

Climate

Longterm annual precipitation since 1956 for this region averages ca. 38 cm (17 in; Western Regional Climate Center, data for Eastonville, CO) with ca. 75% of this occurring from spring rains in April to May and a July–August pulse from thunderstorms. Interannual variation in precipitation can be extreme in Colorado, with severe droughts occurring in the 1950s, 1970s, early 1980s, and early 2000s (Henz et al. 2004). Local rainfall tracks the topographic gradient, where higher elevations near the top of the drainage receive more rainfall in the summer and more winter storm events; these are often highly localized and precipitation events can vary over short distances. Longterm temperature records (Western Regional Climate Center; data for Colorado Springs 1948–2005) indicate an average daily high of 26.6° C (79.9° F) – to an average low of 12.7° C (54.8° F) in the growing season months of June to August, while January temperatures range from an average high of 5.9° C (42.6° F) to a low of 16.6° F (-8.5 C°). These climatic parameters do not differ significantly from those reported by Livingston (1947).

Geology

Livingston (1952) and Branson et al. (1965) noted the relationship between soils of perennial high moisture and the persistence of tallgrass prairie vegetation in Colorado; these azonal conditions are promoted by soil composition and water table dynamics. In our study area, two aquifers play a significant role in local hydrology and soil moisture: the alluvial Black Squirrel Creek aquifer and the underlying andesitic sandstone Dawson Formation bedrock aquifer (Bittenger 1976; Robson 1988; Topper 2008; Morgan & Barkmann 2012). Subsurface topography slopes steeply south, shaped by the ancestral Black Squirrel Creek now covered with glacial alluvium that forms the Black Squirrel Creek aquifer of Pleistocene gravels and coarse sand. This aquifer ranges in depth from 0–215 m; close to the headwaters of Black Squirrel Creek it is relatively shallow but it becomes deeper to the southeast. The alluvial aquifer is a significant source of well water for domestic, agricultural, and municipal uses (Topper 2008) and provides localized high water table occurrences. However, in our

Fig. 3. Main stem of Black Squirrel Creek. Upland areas contain mixed grass prairie vegetation and tallgrass vegetation occurs along the side banks.

study area the alluvial layer is relatively thin or absent, and much of the subsurface water here that supplies the seeps and springs is likely to be primarily a result of the Dawson Formation bedrock aquifer (R. Topper, pers. comm.), a late Cretaceous-Tertiary sandstone widely exposed along the Palmer Divide and close to the surface in the upper Black Squirrel Creek drainage. Becausethe aeolian and alluvial surface deposits of the area are highly permeable, runoff is low, and both aquifers receive recharge from precipitation (Topper 2008). The interface of the alluvial and bedrock aquifers is regionally complex with no detailed mapping of localized hydrological regimes yet available, and it is likely that both the alluvial and bedrock aquifers supply groundwater across the entirety of the drainage.

MATERIALS AND METHODS

The study area was surveyed intensively from May to August 2011 throughout the growing season, although floristic collections occurred regularly since 2000 and sporadically since the 1970s. We conducted qualitative surveys of topography and floristic composition of significant plant communities on each section of the main and subsidiary drainages every two weeks during 2011. We documented the vascular flora as completely as possible, combining new collection with existing recent ones at the Carter Herbarium of Colorado College (COCO); primary voucher specimens for all taxa are at COCO, with duplicates at COLO and CS. Vegetation communities and significant species and wetland features along the main drainage and its key tributaries were mapped using geospatial coordinates.

Our initial surveys along the drainage of Upper Black Squirrel Creek provided qualitative assessments of the current extent and condition of grassland communities in sites as close as possible to those in the original Livingston studies, for which only generalized location information was available. Due to landscape modification in housing developments and roads or inability to obtain permission for access, the most intact communities in which we were able to take quantitative data were located ca. 10 km north of the original Livingston

plains sites, and a similar distance south of his forest-grassland interface plots (Livingston 1947; 1952) within the same hydrologic system in comparable topography. We were able to access the general area where his original sites were located for floristic information, although we did not take quantitative data due to disturbance from intensive grazing and anthropogenic surface alterations.

Livingston utilized nine 100m line transects in seven locations: four sites, each with a single transect, were in the Black Forest within a ponderosa pine-savannah community at 2200–2300 m (7200–7500 ft.), and three locations (one with 3 transects) were along the Black Squirrel Creek drainage in grasslands at ca. 2000 m (6500 ft). The original transects each encompassed ten quadrats of 1 × 0.5 m; in comparison, we used four 105 m transects, each with 20 similarly sized quadrats spaced 5 m apart. This modification allowed us to assess the small-scale heterogeneity characteristic of the region. All 2011 transects were located at approximately 2100 m (7000 ft) in elevation.

Transects 1 and 2 were located along the north-facing bank of the main stem of Black Squirrel Creek (Figs. 2, 3) in vegetation that met our criteria for sufficient length with the presence of tallgrass indicator species *Sporobolus heterolepis, Andropogon gerardii*, *Hesperostipa spartea*, or *Sorghastrum nutans*. These transects were parallel, ca. 10 m apart, and offset so that they overlapped by one half their length. We located two additional transects (Fig. 2) along subsidiary drainages in vegetation with similar criteria: Transect 3 was in a side drainage ca. 1 km north of transects 1 and 2, and Transect 4 was located in a tributary drainage, ca. 3 km north of transect 3. To match the protocol, timing, and data format of Livingston, we surveyed the vegetation in late August following his methodology for assessing basal and relative cover and frequency of dominant taxa.

Basal Cover and Relative Cover

In each quadrat, we estimated the total basal cover as a percentage of the total area, as well as the percent cover of bare ground and litter combined, then averaged these over each transect of 20 quadrats. For each quadrat we estimated the total cover of all plants, the relative cover of combined graminoids (Poaceae, Cyperaceae, Juncaceae and Juncaginaceae) as a percentage of the total vegetative cover, and the contribution of each identifiable species to the total graminoid cover.

Frequency

In each quadrat we recorded the presence of all graminoid species and calculated a frequency metric and rank of the dominant taxa by summing the quadrat data for each transect individually. We also calculated the mean frequency and rank frequency of each species across all transects.

RESULTS

Vascular Flora

The flora reported here (Appendix 1) represented only the hydric and mesic habitats and does not encompass species restricted to the more xeric uplands. Some components of this upland vegetation extended into the drainages, particularly in the open gravels of stream banks and terraces, and are included on the species list, noted as a xeric component. We defined notable elements (Table 1) in four categories. Rare taxa were those tracked as being of conservation concern by the Colorado Natural Heritage Program. Regionally uncommon taxa were those with few regional herbarium records COCO and so categorized in prior studies by Kelso (2012), Culver and Lemly (2013) or Weber and Wittmann (2012). Foothills/Montane elements were topographic disjuncts that typically occur in higher elevation locations of the Pikes Peak or Front Range foothills as noted by Weber and Wittmann (2012) and herbarium records at COCO. Midwestern elements were taxa associated with the characteristic Midwest Prairie flora as explicitly noted by Shantz (1928), Weaver and Fitzpatrick (1934), Weaver (1954), or Livingston (1952).

In the current study, we documented almost 300 taxa representing 62 families as currently recognized in the U.S.D.A. Plants Database (www.plants.usda.gov). The highest species richness was in the Asteraceae (50 species), Poaceae (43 species), Cyperaceae (18 species), and Juncaceae (12 species). Additional families with high species richness included the Fabaceae, Polygonaceae, Rosaceae, and Scrophulariaceae (s. lat.). The flora included relatively few noxious weeds; *Lythrum salicaria*, which existed sporadically in a side drainage of Black

Table 1. Notable plant taxa in the upper Black Squirrel Creek drainage. See Appendix 1 for full nomenclature. Midwest Prairie affiliated species are those so noted by Shantz (1928), Weaver and Fitzpatrick (1934), Weaver (1954) and Livingston (1952). Foothills/Montane distributions in Colorado by Weber and Wittman (2012), and Kelso (2012). Locally uncommon species are from records in COCO and prior fieldwork by Kelso but not tracked statewide by Colorado Natural Heritage Program (CNHP); Rare species are those tracked by the Colorado Natural Heritage Program (2012) as being of conservation concern. CNHP state rarity ratings are as follows: S1= Critically imperiled due to extreme rarity, or factors making it vulnerable to extirpation; 5 or fewer occurrences or less than 1000 remaining individuals; S2=Imperiled, 6–20 occurrences or between 1000–3000 remaining individuals; S3= Vulnerable, 21–100 occurrences or between 3000–10,000 remaining individualsl S4: Apparently secure, uncommon but widespread, with possible longterm concern (www.cnhp.colostate.edu).

Family	Species	Foothills/Montane	Midwest Prairie	Locally Uncommon	Rare
Anacardiaceae	*Toxicodendron rydbergii*	X	X		
Apiaceae	*Cicuta douglasii*		X		
Asclepiadaceae	*Asclepias hallii*	X			X:S3
Asteraceae	*Artemisia ludoviciana*	X	X		
	Cosmos parviflorus			X	
	Erigeron lonchophyllus	X			
	Helenium autumnale	X	X		
	Helianthus pauciflorus		X		
	Liatris ligulistylis		X		X:S1/S2
	Oligoneuron albidum		X		X:S2/S3
	Oligoneuron rigidum		X		
	Packera pseudaurea	X			
	Rudbeckia hirta	X	X		
	Solidago missouriensis		X		
	Solidago nana	X			
	Symphotrichum ericoides		X		
	Symphotrichum laeve	X	X		
	Tripleurospermum perforatum	X			
Brassicaceae	*Arabis holboelii* var. *retrofracta*	X			
	Draba nemorosa	X			
Cactaceae	*Pediocactus simpsonii*	X			
Campanulaceae	*Campanula rotundifolia*	X			
	Lobelia siphilitica		X	X	
Caryophyllaceae	*Stellaria longifolia*	X			
Clusiaceae	*Hypericum scouleri*	X		X	
Cyperaceae	*Carex aurea*	X		X	
	Carex crawei	X			X:S1
	Carex disperma	X			
	Carex echinata	X		X	
	Carex simulata	X		X	
	Eleocharis quinqueflora	X		X	
Equisetaceae	*Equisetum arvense*	X			
Fabaceae	*Astragalus canadensis*		X	X	
	Dalea candida		X		
	Dalea purpurea		X		
	Glycyrrhiza lepidota		X		
Gentianaceae	*Gentianopsis amarella* (*strictiflora* type)	X			X*
	Gentianopsis virgata		X		(not yet CNHP rated)
Hippuridaceae	*Hippuris vulgaris*	X			
Iridaceae	*Hypoxis hirsuta*		X		X:S1
Juncaceae	*Juncus brachycephalus*		X		X:S1
	Juncus brevicaudatus		X		X:S1
Juncaginaceae	*Triglochin palustris*	X			
Lamiaceae	*Lycopus americanus*		X		
	Monarda fistulosa		X		
	Scutellaria galericulata			X	
Lentibulariaceae	*Utricularia minor*	X			X:S2
Liliaceae	*Lilium philadelphicum*	X	X		X:S3/S4
Malvaceae	*Sidalcea neomexicana*	X		X	
Onagraceae	*Gayophytum diffusum*	X			
	Oenothera flava			X	

Table 1. Continued

Family	Species	Foothills/Montane	Midwest Prairie	Locally Uncommon	Rare
Orchidaceae	*Platanthera aquilonis*	X			
	Spiranthes romanzoffiana	X		X	
Poaceae	*Agropyron cristatum*		X		
	Agrostis scabra	X			
	Alopecurus aequalis	X			
	Andropogon gerardii		X		
	Bouteloua curtipendula		X		
	Calamagrostis stricta	X			
	Calamovilfa longifolia		X		
	Elymus canadensis		X		
	Glyceria elata	X			
	Glyceria striata	X			
	Hesperostipa spartea		X	X	
	Koeleria macrantha	X	X		
	Muhlenbergia montana	X			
	Panicum virgatum		X		
	Poa fendleriana	X			
	Poa nemoralis ssp. *interior*	X	X		
	Poa pratensis				
	Schizachyrium scoparium		X	X	
	Sorghastrum nutans		X	X	
	Sporobolus heterolepis		X	X	
Polygonaceae	*Polygonum amphibium*		X		
Primulaceae	*Dodecatheon pulchellum*	X			
	Lysimachia ciliata		X	X	
Ranunculaceae	*Anemone canadensis*	XX	X		
	Anemone cylindrica	X	X		
Rosaceae	*Agrimonia striata*	X		X	
	Geum aleppicum	X			
	Potentilla arguta	X			
	Rosa arkansana		X		
Rubiaceae	*Galium boreale*	X			
	Galium trifidum	X			
Salicaceae	*Populus angustifolia*	X			
	Salix irrorata	X			
Selaginaceae	*Selaginella densa*	X			
Scrophulariaceae	*Nuttallanthus canadensis*			X	
	Pedicularis canadensis	X			
	Penstemon glaber	X			
	Penstemon gracilis		X	X	
	Veronica serpyllifolia	X			
Sparganiaceae	*Sparganium angustifolium*	X			
Valerianceae	*Valeriana edulis*	X			
Violaceae	*Viola sororia*	X	X		

Squirrel Creek, is the only A list species. Although a detailed floristic list was not an objective of the Livingston studies, we found almost all taxa he noted as still present, with only a few exceptions (Appendix 1).

Over one fifth of the flora was regionally associated with foothills/montane habitats, and at least a comparable proportion was characteristic of the Midwest prairies. By contemporary phytogeographic perspectives and greater documentation of the Great Plains flora, the Midwest association was almost certainly an underestimate, but to simplify comparison, we used for reference only those species explicitly listed in early studies as characteristic of the Midwest. Eight of the "Midwest" species were also locally characteristic of the foothills/montane zone. Eighteen plant species occurring in the Black Squirrel Creek drainage were locally uncommon, and nine were tracked by the Colorado Natural Heritage Program for being of conservation concern.

Wetland habitat Classifications

We identified eight general wetland habitat types characterized by distinct hydrogeomorphic characteristics and floristic profiles (Table 2). Our classification follows the Colorado Natural Heritage Program (Carsey et al. 2003) and includes general categories of Riverine Wetlands sourced by ongoing streamflow, Slope Wetlands supported by groundwater on gentle to moderate slopes, and Depressional Wetlands supported by ground water filling a depression on a permanent or intermittent basis. Each habitat type occurs in multiple instances throughout the Black Squirrel drainage. Vegetation associations listed for each hydrogeomorphic class follow those used by the Colorado Natural Heritage Program (Carsey et al. 2003; Culver & Lemley 2013) classifications as closely as possible.

Riverine Wetlands

Stream Channel Tall Willow Shrubland.—This community occurred in a limited extent on the northwestern edge of the main Black Squirrel Creek drainage, covering about a kilometer in length; shrub cover diminished further downstream, but reoccured in patches along the drainage in wide stream meanders with shallow subsurface water. The primary vegetation community was sandbar willow-mesic graminoid shrubland dominated by *Salix exigua* with occasional occurrences of other tree and shrub species of willow (e.g., *S. irrorata, S. ligulifolia,* and *S. amygdaloides*); the forb component was limited but included patchy occurrences of *Agrimonia striata, Cirsium canadensis, Glycyrrhiza lepidota, Helianthus nuttallii, Monarda fistulosa,* and *Rudbeckia hirta.*

Stream Channel Herbaceous Vegetation.—Open gravels of the main channel and occasional side drainages supported a linear strip of obligate wetland forbs, sedges, and rushes where stream flow formed riffles around gravel banks and sandbars. The gravel stream channels were notable for their abundance and diversity of rushes, including the rare *Juncus brachycephalus*, as well as *Gentianopsis virgata.* Both of these species are Midwest prairie elements known in Colorado only from this region. Although dominated by non-woody vegetation, the stream channels also supported occasional occurrences of young saplings of *Populus deltoides* or species of *Salix.*

Slope Wetlands

Moist Shelves.—These heterogeneous surfaces were located primarily in the main drainage above the creek channel depression and along some subsidiary drainages. Surfaces were flat to gently sloping, with moisture accumulating from springs and runoff above. Moister areas held a greater abundance of facultative or obligate wetland species interspersed with xeric elements. Vegetative cover was primarily composed of graminoids and mixed forbs with occasional shrub patches. *Sporobolus heterolepis* was particularly widespread here, and the shelves supported extensive occurrences of a *Sporobolus heterolepis* dominated community with occasional instances of *Andropogon gerardii*, along with patches of *Andropogon gerardii-Sorghastrum nutans* associations. The *Sporobolus*-dominated communities ranged in width from 5 m to almost 40 m; depending on the topography, lengths could be short patches of 10 m to longer extents over 50 m. Drier areas included heterogeneous mixed grass vegetation with *Calamovilfa longifolia, Koeleria macrantha, Muhlenbergia montana, Poa pratensis,* and *Schizachyrium scoparium.*

Moist Banks.—These encompassed a significant portion of the drainage system and held some of the highest diversity of forbs. One of the most significant species occurring here was the locally abundant, state-rare *Liatris ligulistylis.* The moist banks typically occurred on side drainages with a U-shape profile and received consistent subsurface moisture from seeps and springs; their surfaces were steeper than moist shelf habitats, and they usually included seeps that oozed perennial moisture. Plant associations included mixed mesic tallgrass communities with components of *Calamovilfa longifolia, Schizachyrium scoparium, Sorghastrum nutans, Sporobolus heterolepis,* and *Stipa spartea. Andropogon gerardii* clumps were common, but did not form a dominant component of the vegetative cover. Like moist shelf communities, bank communities sometimes occurred as lengthy strips to 50 or more meters, or as shorter patches interspersed with depressional wetlands.

Depressional wetlands

Nebraska Sedge Bogs and Meadows.—These associated habitats were both dominated by *Carex nebrascensis* and

TABLE 2. Common floristic elements in wetland communities of the Black Squirrel Creek drainage. For full nomenclature see Appendix 1.

	Graminoids	Forbs	Shrubs
RIVERINE WETLANDS			
Stream Channel Tall Willow Shrubland		*Agrimonia striata*	*Salix exigua*
		Helianthus nuttallii	*Salix irrorata*
	Monarda fistulosa		*Salix ligulifolia*
	Rudbeckia hirta		
'Stream Channel Herbaceous Wetlands	*Juncus alpinoarticulatus*	*Epilobium ciliatum*	
	Juncus brachycephalus	*Gentianella strictiflora*	
	Juncus dudleyi	*Gentianopsis virgata*	
	Juncus interior	*Onosmodium bejariense*	
	Juncus saximontanus	*Veronica anagallis-aquatica*	
	Juncus torreyi		
SLOPE WETLANDS			
Moist Shelves	*Andropogon gerardii*	*Antennaria microphylla*	*Rosa arkansana*
	Calamagrostis stricta	*Astragalus canadensis*	*Symphoricarpos occidentalis*
	Elymus lanceolatus	*Erigeron bellidiastrum*	
	Juncus arcticus	*Fragaria vesca*	
	Poa pratensis	*Geum aleppicum*	
	Schizachyrium scoparium	*Glycyrrhiza lepidota*	
	Helianthus nuttallii		
	Monarda fistulosa		
	Pedicularis canadensis		
	Ratibida columnifera		
	Rudbeckia hirta		
'Moist Banks	*Andropogon gerardii*	*Collomia linearis*	
	Poa pratensis	*Geum aleppicum*	
	Sorghastrum nutans	*Helenium autumnale*	
	Stipa spartea	*Helianthus nuttallii*	
	Liatris ligulistylis		
	Potentilla arguta		
	Prunella vulgaris		
	Rudbeckia hirta		
	Thermopsis montana		
	Viola sororia		
DEPRESSIONAL WETLANDS			
Sedge Meadows & Bogs	*Carex nebrascensis*	*Epilobium leptophyllum*	
	Glyceria elata	*Lobelia siphilitica*	
	Glyceria striata	*Mentha arvensis*	
	Juncus nodosus	*Polygonum pensylvanicum*	
	Juncus saximontanus	*Polygonum punctatum*	
	Juncus torreyi	*Scutellaria galericulata*	
	Poa leptocoma	*Stellararia longifolia*	
Open Seeps	*Carex aurea*	*Hypoxis hirsuta*	
	Carex crawei	*Spiranthes romanzoffiana*	
	Carex xerantica	*Dodecatheon pulchellum*	
	Eleocharis quinqueflora	*Gentianopsis virgata*	
	Juncus alpinoarticulatus	*Parnassia palustris*	
	Triglochin maritima	*Platanthera aquilonis*	
	Triglochin palustris	*Sisyrinchium montanum*	
Fens	*Carex simulata*	*Helenium autumnale*	
	Eleocharis acicularis		
	Scirpus pungens		
Ponds	*Scirpus microcarpus*	*Alisma triviale*	
		Hippuris vulgaris	
		Polygonum amphibium	
		Potamogeton natans	
		Ranunculus trichophyllus	
		Sagittaria cuneata	
		Sagittaria latifolia	
		Sparganium angustifolium	
		Utricularia minor	

typically occurred adjacent to streams and marshy areas with a high water table overlain by a layer of sediment and organic material. In the bogs, *Glyceria* was often present, along with a limited number of forbs such as members of the Polygonaceae and *Helenium autumnale*. Tributary channels above the water flow of drainage bottoms supported the more abundant sedge meadow community, which also occurred along shallow channels with no visible surface water. Sedge meadows were drier and more floristically diverse in hydrophytic graminoids, with Nebraska sedge occurring along with *Juncus arcticus*, other sedge species such as *Carex disperma*, as well as bulrush species in *Scirpus* and *Schoenoplectus*. Forbs included hydrophytes such as *Lobelia siphilitica* and *Scutellaria galericulata*, both regionally uncommon but locally abundant here, as well as the widespread *Mentha arvensis* and representatives of the Polygonaceae.

Open Seeps.—Open seeps underlain by clay lenses occurred frequently throughout the drainage system. Groundwater emerged through the soil to create a shallow layer of standing water 1–2 cm deep over saturated clay-rich mud with little to no vegetative cover. Seeps ranged from ca. 1 m^2 to 100 m^2 in area and were located above stream level along shallow bank margins. The surfaces were dotted with low hummocks, vegetation-covered mounds from 10 to 50 cm in height and width. These habitats encompassed an unusual flora composed of species more typical of higher elevations (e.g., *Dodecatheon pulchellum, Eleocharis quinqueflora,* and *Parnassia palustris*) along with a number of state-rare species, all Midwest prairie elements, such as *Carex crawei, Gentianopsis virgata,* and *Hypoxis hirsuta.*

Fens.—This habitat type was a significant wetland community because only a few are known east of the Front Range, although diverse types occur commonly in higher elevations. Fens are characterized by a deep, subsurface peat layer (Culver & Lemly 2013) and abundant *Carex simulata*. A *C. simulata* matrix is characteristic of higher elevation fens and indicative of peatland development (Culver and Lemly 2013). The largest Black Squirrel Creek fen covered ca. 400 m^2 in a subsidiary drainage north of the main channel below a large open seep. It was characterized by *Carex simulata* mats with occasional occurrences of *Eleocharis acicularis, Carex nebrascensis,* and *Schoenoplectus pungens*. The few forbs present included *Helenium autumnale* and *Parnassia palustris*. Soils were highly saturated and visibly quaked when stepped upon; the underlying peat layer was over a meter thick. Smaller apparent fens where the vegetation was dominated by *C. simulata* occurred sporadically in subsidiary wet drainages.

Ponds.—A number of small ponds occurred throughout the drainages. These are generally less than 9.3 m^2 (ca. 100 ft. ^{2}) in area, with a depth of 0.3 m (1 ft) to over 1.5 m (4 ft), depending on precipitation. The ponds supported abundant amphibians, aquatic insects, crustaceans, and other larger vertebrates such as minnows, along with diverse floating and emergent plant species. Pond associations included an emergent *Typha* marsh community, and a floating aquatic community with the carnivorous species *Utricularia minor* in shallow ponds, along with more common aquatics such as *Sagittaria, Alisma, Sparganium,* and *Potamogeton.*

Vegetation transects

Vegetative and Graminoid Cover.—Transects were situated primarily on moist banks and moist shelves, although they also encompassed Nebraska sedge meadows and bogs as well as open seeps (Fig. 2). They varied in their vegetative cover and the relative cover of graminoids, forbs, or litter/bare ground (Table 3; Fig. 4). On average, total basal vegetative cover was slightly over 50%, and graminoids constituted almost 80% relative cover. The dominant grass contributors to cover (in order of prominence: *Sporobolus heterolepis, Muhlenbergia montana, Schizachyrium scoparium, Sorghastrum nutans,* and *Calamovilfa longifolia;* Table 4) parallelled key components documented by Livingston (1952). Common but lesser contributors in both studies included *Andropogon gerardii, Hesperostipa spartea,* and *Panicum virgatum.*

Variation among the transect quadrats reflected the characteristic local heterogeneity of patchy clumps of vegetation interspersed with open soil. Transect 1 was the most hydric, with abundant subsurface water and a small seep dominated by *Juncus arcticus*. It had the highest overall cover, primarily *Sorghastrum nutans, Sporobolus heterolepis,* and *Schizachyrium scoparium,* with lesser components of *Muhlenbergia montana, Bouteloua gracilis, Calamovilfa longifolia, Panicum virgatum,* and *Koeleria macrantha.*

Although adjacent to transect 1, transect 2 showed somewhat different community structure where the

TABLE 3. Comparison of total vegetative cover and relative cover of dominant graminoid species, 2011 and Livingston studies of the 1940s. T1–T4 represent 2011 transects. L1–L7 represent data from Livingston (1947, 1952; 1952 transect numbers modified from those used in 1947).

	T1	T2	T3	T4	Mean All Transects
Total % Vegetative Cover	63.8	58.8	46.5	43.8	53.2
Relative % Cover All Graminoids	69.5	77.7	86.5	85.7	79.9
Dominant Grasses (% Relative Cover)	*Sorghastrum nutans* (12) *Sporobolus heterolepis* (9) *Schyzachyrium scoparium* (7.5) *Bouteloua* sp. (4.5) *Muhlenbergia montana* (4.2) *Calamovilfa longifolia* (3.2) *Panicum virgatum* (2.8) *Koeleria macrantha* (0.7)	*Sorghastrum nutans* (25.3) *Schizachyrium scoparium* (20.2) *Muhlenbergia montana* (8.9) *Calamovilfa longifolia* (7.4) *Sporobolus heterolepis* (7.2) *Bouteloua gracilis* (1.3) *Hesperostipa spartea* (1.2) *Nasella viridula* (1)	*Sporobolus heterolepis* (27.1) *Calamovilfa longifolia* (20) *Andropogon gerardii* (12) *Bouteloua gracilis* (8.9) *Muhlenbergia montana* (4.9) *Schizachyrium scoparium* (0.9)	*Muhlenbergia montana* (36.8) *Sporobolus heterolepis* (18.7) *Schizachyrium scoparium* (17.5) *Hesperostipa spartea* (3.9) *Sorghastrum nutans* (3)	*Sporobolus heterolepis* (15.1) *Muhlenbergia montana* (13.2) *Schizachyrium scoparium* (11) *Sorghastrum nutans* (10.7) *Calamovilfa longifolia* (7.8)
Forest	**L1**	**L2**	**L3**	**L4**	**Mean**
Dominant Grasses (% Relative Cover)	*Poa pratensis* (31.4) *Sporobolus heterolepis* (29.1) *Muhlenbergia montana* (4.9)	*Bouteloua gracilis* (14.2) *Poa compressa* (10.5) *Sporobolus heterolepis* (10.1)	*Sporobolus heterolepis* (33.9) *Muhlenbergia montana* (9.3) *Bouleloua gracilis* (6.8)	*Sporobolus heterolepis* (73.4) *Poa pratensis* (4.6)	*Sporobolus heterolepis* (36.7) *Poa pratensis* (9) *Bouteloua gracilis* (5.3) *Muhlenbergia montana* (3.5)
Plains	**L5**	**L6**	**L7U/M/L**		**Mean**
Dominant Grasses (% Relative Cover)	*Andropogon gerardii* (28.2) *Bouteloua gracilis* (19.8) *Sporobolus heterolepis* (12.5) *Calamovilfa longifolia* (8.1)	*Sporobolus heterolepis* (30.7) *Schizachyrium scoparium* (25.3) *Elymus trachycaulus* (8.0) *Andropogon gerardii* (5.2)	*Schizachyrium scoparium* (47.2/28.7/55.8) *Bouteloua gracilis* (31.0/4.9/15) *Calamovilfa longifolia* (10.6/0/0.8) *Sorghastrum nutans* (0.3/30.7/2.1)		*Sporobolus heterolepis* (35) *Schizachyrium scoparium* (31.4) *Bouteloua gracilis* (15) *Calamovilfa longifolia* (7.6) *Andropogon gerardii* (6.7)

microtopography of the terraces contributed to variable soil moisture and texture. This transect was also dominated by *Sorghastrum nutans*, contributing ca. 25% of the vegetative cover, with *Schizachyrium scoparium* contributing an additional 20%. *Sporobolus heterolepis* contributed considerably lesser cover here (7%). In general, this transect showed a greater presence of more xeric elements such as *Muhlenbergia montana* and *Calamovilfa longifolia* than transect 1 above it, and somewhat less overall cover.

Transect 3, in a side drainage adjacent to the main channel, had comparatively lower cover than transects 1 and 2, less than 50% overall; 90% of this cover was composed of grasses dominated by *Sporobolus heterolepis*, *Calamovilfa longifolia* and *Andropogon gerardii*. Together these species accounted for ca. 59% relative cover. This was the only transect in which *A. gerardii* appeared to a notable extent, contributing 12% relative cover.

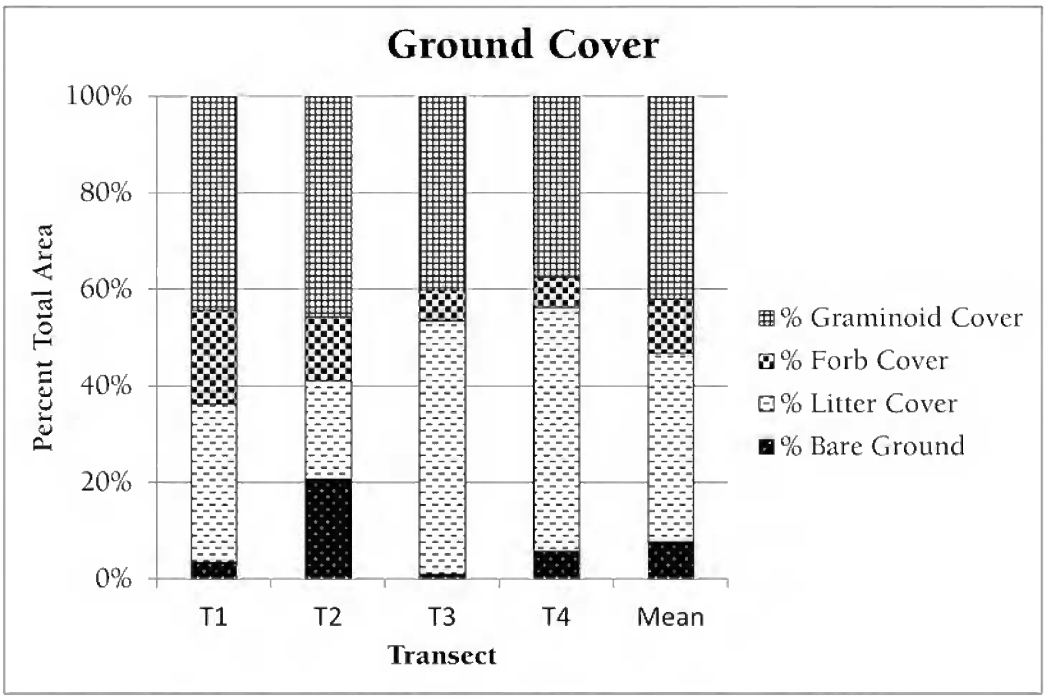

Fig. 4. Percent ground cover of graminoids, forbs, litter and bare ground for 2011 transects. T1–4 refers to transect numbers as described in the text.

Table 4. Comparison of the highest frequency grasses in the Livingston (1947; 1952) study and 2011. T1–T4 are 2011 transects; L1, L4, L5, and L6 are Livingston data from 1947, republished in 1952. No frequency data were given for transects L2, L3, and L7. Livingston stations L1–L4 were located in the Black Forest ("forest stations" sensu Livingston) and stations L5–L6 were "plains" transects. 2011 transects were located midway in distance and elevation between the forest and plains transects.

Species	T1	T2	T3	T4	Mean %F in 2011 (rank)	L1	L4	Mean %F-forest 1952 (rank)	L5	L6	Mean %F – plains 1952 (rank)
Andropogon gerardii	0	0	35	0	9(8)	10	10	10(6)	70	30	50(4)
Bouteloua gracilis	0	20	30	10	15(6)	0	0	0	100	30	65(2)
Calamovilfa longifolia	20	50	50	20	35(4)	0	0	0	90	30	60(3)
Hesperostipa spartea	0	15	0	50	11(7)	40	10	25 (5)	0	0	0
Koeleria macrantha	15	0	0	0	4(9)	10	50	30(4)	30	10	20(6)
Muhlenbergia montana	15	40	35	80	43(1)	80	20	50(3)	40	0	20 (6)
Panicum virgatum	5	0	5	0	3(10)	0	0	0	10	30	20(6)
Poa pratensis	5	10	0	20	9(8)	80	40	60(2)	0	0	0
Schizachyrium scoparium	30	60	10	50	38(2)	10	0	5(7)	95	90	93(1)
Sorghastrum nutans	55	80	0	10	36(3)	0	0	0	15	30	23(5)
Sporobolus heterolepis	25	25	50	35	34(5)	70	100	85(1)	40	100	60(3)

In transect 4, located in a large subsidiary drainage with a perennial secondary stream, vegetative cover was also less than 50%, and composed primarily of *Muhlenbergia montana, Sporobolus heterolepis,* and *Schizachyrium scoparium*; together these species comprised 73% of the graminoid cover. *Hesperostipa spartea* and *Sorghastrum nutans* were more frequent here than in the other transects, although they contributed relatively little to cover. Both species are regionally uncommon to rare (but not considered rare statewide), and when present, they typically occur in disparate clumps. This characteristic pattern was apparent in transect 4,

and underscored the decoupled metrics of a species contribution to cover from overall frequency of occurrence for individual species in these communities.

Grass Species Frequency Rankings

Across all transects, the most common species (Table 3) were *Muhlenbergia montana* (frequency of ca. 42% of all quadrats), *Schizachyrium scoparium* (37% frequency), *Sorghastrum nutans* (36% frequency), *Calamovilfa longifolia* (35% frequency), *Sporobolus heterolepis* (34% frequency), and *Juncus arcticus* (32% frequency). Grass taxa of second tier frequency included *Hesperostipa spartea* (16% frequency), *Bouteloua gracilis* (15% frequency), *Andropogon gerardii* (9% frequency), and *Poa pratensis* (9% frequency). The highest frequency non-graminoid taxa (data not shown) included a high representation of Midwest prairie elements, notably *Artemisia ludoviciana, Dalea purpurea, Equisetum arvense, Glycyrrhiza lepidota, Helenium autumnale, Oligoneuron rigidum, Rosa arkansana, Symphotrichum ericoides,* and *Symphotrichum laeve.* These species were common components of the regional mixed grass prairie; only *Helenium autumnale* is an elevational disjunct more common in the Foothills/Montane zone than on the plains.

DISCUSSION

Comparison of Grassland Vegetation Structure: 1940s and 2011

Both studies document considerable variation within and among transects and the overall means cover wide ranges at both time frames (Table 3). We found considerably higher basal vegetative cover (typically over 50%) than what Livingston reported (typically less than 20%). In 2011, graminoids constituted ca. 80% of this cover, while on the Livingston forest-grassland plots, 85% of this cover was constituted by graminoids, and on the plains plots, 55%. The dominant grasses were similar, with *Sporobolus heterolepis* being the top contributor to cover in both studies. In 2011, *Muhlenbergia montana, Schizachyrium scoparium, Sorghastrum nutans,* and *Calamovilfa longifolia* were also important components; jointly these provided 60% relative cover. In the Livingston study, in addition to *S. heterolepsis* (55% relative cover), *Poa pratensis, Bouteloua gracilis,* and *M. montana* contributed most highly on the forest transects while *S. scoparium, B. gracilis, C. longifolia, and A. gerardii* played key secondary roles on the plains (95% relative cover).

Comparison of the frequency of species occurrence (Table 4) provides a similar picture of a consistent suite of species common to both time frames, albeit with different rankings for individual frequencies. *Muhlenbergia montana, Schizachyrium scoparium, Sorghastrum nutans, Calamovilfa longifolia,* and *Sporobolus heterolepis* were the most commonly occurring species in 2011, each present in over 30% of the quadrats. On the Livingston forest plots, *S. heterolepis, Poa pratensis, M. montana,* and *Koeleria macrantha* were most frequently encountered, while on the plains, *S. scoparium, B. gracilis, S. heterolepis, C. longifolia,* and *A. gerardii* each occurred in at least 50% of the quadrats.

The 2011 structure of the tallgrass vegetation of Black Squirrel Creek remained strongly comparable to what Livingston described in the 1940s with respect to the most frequent grass species and those that contributed the most cover. Key species in the 1940s (in particular, *Sporobolus heterolepis, Muhlenbergia montana, Schizachyrium scoparium,* and *Sorghastrum nutans*) remained important now. *Andropogon gerardii* seems to have diminished in both frequency and contribution to cover since the 1940s, although even then it was not a dominant component of the vegetation. However, because the Livingston transects could not be precisely relocated, our transect positions did not match his sample sites, and at least some of these differences may be artifacts of different transect positions. Other differences may result from limited sampling in a landscape mosaic where topography, edaphic factors, and at least to some extent, current and past grazing practices, create patchy vegetation or bare ground. Because our plots had light grazing and no mowing (in comparison to the Livingston plots that were subjected to grazing and seasonal mowing), this may have allowed for greater cover to develop in some areas. Alternatively, these differences may reflect real changes in species abundance. Possible considerations include recovery lag from the 1930s Dust Bowl decade that might have exerted a lingering effect during the 1940s, or the converse, when several substantial drought episodes in the intervening decades since the Livingston work may have influenced the response and recovery of individual species.

Although Livingston's characterization of Midwestern grasslands as "true prairie" may be arguable, his analogy of the Black Squirrel Creek vegetation to the Midwestern grasslands was then, and remains now, appropriate with respect to the major grasses present and their relative contributions to cover, as well as to the forb and shrub elements in the flora and vegetation structure. However, this vegetation is not identical to iconic tallgrass associations of the central prairies and identified elsewhere in Colorado, where *Andropogon gerardii* is the signature species with the highest cover and frequency (Moir 1972; Bock & Bock 1998; Neid et al. 2009). In the Black Squirrel Creek associations, while *A. gerardii* never contributed highly to cover, it occurred relatively frequently. The most prominent grass was *Sporobolus heterolepis,* occurring with foothills/montane species such as *Muhlenbergia montana* and xeric or mixed grass prairie species such as *Calamovilfa longifolia* and *Bouteloua gracilis.* The Black Squirrel Creek vegetation may be better described as *Sporobolus heterolepis–Muhlenbergia montana* grasslands with subsidiary components of *Calamovilfa longifolia, Schizachyrium scoparium,* or *Sorghastrum nutans* rather than the more classical model of tallgrass communities defined by the dominance of *A. gerardii*. No comparable associations dominated by *Sporobolus heterolepis* are currently listed by NatureServe (2013), or documented in Colorado, although Weaver (1954) described prairie dropseed communities as a distinctive, albeit minor, component of xeric upland prairie on the midwestern plains.

The Wetland-Grassland Mosaic

We concur with the conclusion reached by Livingston (1952) specifically for the Black Squirrel Creek/Black Forest area, and Branson et al. (1965) more broadly for the Colorado mountain front, that adequately high soil moisture is the key factor responsible for the occurrence of mesic tallgrass prairie. As transitional zones between aquatic and terrestrial habitats, wetlands play vital roles in linking ecological and hydrological systems (Culver and Lemly 2013) and are widely recognized for having high biological significance due to their variety of biodiversity and community types; this is particularly true in the arid Arkansas River drainage of Pueblo and El Paso Counties (Doyle et al. 2001b) where few wetlands presently occur. In the Black Squirrel Creek drainage, the wetlands were a critical part of the vegetation mosaic of hydric and mesic communities and entwined biota. As noted in other prairie systems (Semlitsch and Bodie 1998; Leibowitz 2003), even small and superficially discontinuous imbedded wetlands support metapopulation, corridor, seasonal or annual habitat dynamics for flora and fauna by connecting subsurface geology and hydrology. In the Black Squirrel Creek drainage, this connectivity sustains the anomalous vegetation and flora and is certainly part of their longevity.

A conclusion of botanical stasis along Black Squirrel Creek is not appropriate, however. Change has occurred, perhaps with respect to change in frequency of certain species, but certainly visibly with respect to extent of these grasslands, which now exist as remnants reduced in both number and size since the 1940s, and even by then probably reduced from their former extent prior to extensive ranching (Livingston 1952). Where widespread mesic grasslands once prevailed, housing developments and infrastructure or altered grasslands with adventive, grazing- tolerant, or xeric species sometimes now dominate. In spite of these alterations and diminished extent of communities flagged as noteworthy 70 years ago, the Black Squirrel Creek drainage remains a remarkable center of biotic diversity increasingly significant for its numerous rare or uncommon species, and its elevational and longitudinal disjuncts. Its unique grasslands show clear affiliation to their geographically and temporally distant cousins that are not structurally identical but nonetheless strongly conspecific in their floristic profiles.

Although it remains speculative that these communities are *in situ* Pleistocene relicts, they have endured substantial climatic vicissitudes. In the past century, interannual droughts have occurred regularly, and severe droughts within the context of these comparative studies show little apparent major impact in areas directly supported by ground water. Where this vegetation remains, the Black Squirrel Creek drainage testifies to the capacity of hydrogeomorphic systems to sustain relative stasis in prairie plant communities and their constituent flora through fluctuating temperature and moisture regimes. Whether this system can be self-sustaining through accelerating anthropogenic and climatic pressures remains an open question and concern.

APPENDIX 1
ANNOTATED CHECKLIST OF THE VASCULAR FLORA
UPPER BLACK SQUIRREL CREEK DRAINAGE, EL PASO CO., COLORADO

Species list for vascular flora occurring in mesic and hydric communities of the upper Black Squirrel Creek drainage from 7000–6500 feet in elevation. The list includes some upland species occurring sporadically in the drainage system and gravel stream channels, but which are more typically found in the surrounding xeric mixed grass and shortgrass matrix in the surrounding uplands. Nomenclature (including family designations) and common names follow the National Resource Conservation Service database (www. Plants.USDA.gov: accessed 8/2013) except as noted. Nomenclature used in Colorado (e.g., Weber & Wittmann 2012) is given in curly braces as {name} prior to the common name. Alternative Angiosperm Phylogeny Group familial designations (APG; www.mobot.org/MOBOT/Research/APweb) are included for each family. Voucher specimens for all taxa are at COCO. Noteworthy species are coded as follows:

FM Species generally occurring in Foothills/Montane zone 2000–3200 m (ca. 7000–10,500 ft). Distributions follow Weber and Wittman 2012; Culver and Lemly 2013; Kelso, 2012); occurrence on the prairie is restricted.

MWP Species prominent in Midwest prairie as explicitly noted by Shantz (1923), Weaver and Fitzpatrick (1934: Tables 15; 16), Weaver (1954), and Livingston (1952). Earlier nomenclature used in these publications cross-referenced with NRCS Plants Database synonyms.

R Rare species listed as of conservation concern and tracked by the Colorado Natural Heritage Program (2012): State Conservation rankings are as follows: S1: Critically Imperiled, S2: Imperiled, S3: Vulnerable

U Locally or regionally uncommon or local endemic (Kelso 2012; Weber & Wittmann 2012)

X Xeric element of uplands extending into mesic vegetation

L indicates a species noted in the Livingston studies; square brackets indicates a species observed but not recollected in our study. Unless otherwise noted, these are locally common components of the xeric plains flora. Livingston species not observed are so indicated.

Species with no coding are locally widespread components of regional vegetation.

Amaranthaceae
Froehlichia gracilis (Hook.) Moq. (slender snakecotton) **X**

Alismataceae
Sagittaria cuneata Sheldon (arumleaf arrowhead)
Sagittaria latifolia Willd. (broadleaf arrowhead)
Alisma triviale Pursh (northern water plaintain)

Anacardiaceae
Toxicodendron rydbergii (Small) Greene (poison ivy) **FM, MWP**

Apiaceae
Cicuta douglasii (D.C.) J.M. Coulter & Rose (western water hemlock) **MWP**
Berula erecta (Hudson) Coville (cutleaf water parsnip)

Apocynaceae
Apocynum cannabinum L. (Indianhemp)

Asclepiadaceae (APG Apocynaceae)
Asclepias hallii A. Gray (Hall's milkweed) **R (S3), FM**
Asclepias speciosa Torr. (showy milkweed)

Asteraceae
Achillea millefolium L. (common yarrow) **L**
Agoseris glauca (Pursh) Raf. (pale agoseris)
[*Ambrosia artemisiifolia* L. (annual ragweed) **L]**
Ambrosia psilostachya DC. (Cuman ragweed) **X**
Antennaria microphylla Rydb. (littleleaf pussytoes) **X; L** as *A. parviflora*
[*Artemisia campestris* L. ssp. *caudata* (Michx.) Hall & Clements (field sagewort) **L]**
Artemisia frigida Willd. (prairie sagewort) **X, L**
Artemisia ludoviciana Nutt. (white sagebrush) **MWP, L** as *A.gnaphalodes*
Bahia dissecta (A. Gray) Britton (ragleaf bahia) **X**
Bidens tenuisecta A. Gray (slimlobe beggarticks)
Carduus nutans L. (nodding plumeless thistle) Noxious weed of limited occurrence on the study site; few individuals.
Cirsium arvense (L.) Scop. {*Breea arvense*} (Canada thistle) Noxious weed of limited occurrence on the study site
Cirsium flodmanii (Rydb.) Arthur (Flodman's thistle)
Conyza canadensis (L.) Cronquist (Canadian horseweed) **L** as *Leptilon canadensis*
Cosmos parviflorus (Jacq.) (southwestern cosmos) **U** Southwestern species known primarily as regional endemic to the Black Forest region; locally common along Black Squirrel Creek on gravelly stream channels.
Erigeron bellidiastrum Nutt. (western daisy fleabane)
Erigeron compositus Pursh (cutleaf daisy) **FM**
Erigeron divergens Torr. & A. Gray (spreading fleabane)
Erigeron flagellaris A. Gray (trailing fleabane)
Erigeron glabellus Nutt. (streamside fleabane)
Erigeron lonchophyllus Hook. {*Trimorpha lonchophylla*} **FM**
Erigeron subtrinervis Rydb. ex Porter & Britton (threenerve fleabane)
Erigeron vetensis Rydb. (early bluetop fleabane) **FM**
Grindelia squarrosa Dunal (curlycup gumweed)
Helenium autumnale L. (common sneezeweed) **FM, MWP, L**
Helianthus annuus L. (common sunflower)
Helianthus nuttallii Torr. & A. Gray (Nuttall's sunflower)
Helianthus petiolaris Nutt. (prairie sunflower) **L**

Helianthus pumilus Nutt. (little sunflower)
Helianthus pauciflorus Nutt. ssp. (Rydb.) O. Spring. & E. Schilling {*Helianthus rigidus*} (stiff sunflower) **MWP, L**
Heterotheca canescens (D.C.) Shinners (hoary false goldenaster) **L** as *Chrysopsis villosa*
Lactuca tatarica (L.) Meyer (blue lettuce)
Liatris ligulistylis (A. Nelson) K. Schum. (Rocky Mountain blazingstar) **R (S1/S2), MWP, L** Common in seeps and tallgrass communities on the study site.
Liatris punctata Hook. (dotted blazingstar) **MWP, L**
*Lygodesmia juncea (*Pursh) D. Don ex Hook. (rush skeletonplant)
Oligoneuron album (Nutt.) G.L. Nesom {*Unamia alba*} (prairie goldenrod) **R (S2/S3), MWP, L**
Oligoneuron rigidum (L.) Small (stiff goldenrod) **MWP, L** as *Solidago rigidum*
[Packera neomexicana (A. Gray) W.A. Weber & Á. Löve var. mutabilis (Greene) W.A. Weber & Á. Löve (New Mexico groundsel) **L** as *Senecio mutabilis*)
Packera pseudaurea (Rydb.) W.A. Weber & A. Löve (falsegold groundsel) **FM**
Packera tridenticulata (Rydb.) W.A. Weber & A. Löve (threetooth ragwort)
Pseudognaphalium canescens (D.C.) W.A. Weber (Wright's cudweed)
Ratibida columnifera (Nutt.) Woot. & Standl. (upright prairie coneflower)
Rudbeckia hirta L. (black eyed Susan) **FM, MWP, L**
[*Salsola tragus* L. (prickly Russian thistle] **L** as *Salsola pestifer*]
Schkuhria multiflora Hook. & Arn. (manyflower false threadleaf) **X**
Senecio spartioides Torr. & A. Gray (broomleaf ragwort)
Solidago gigantea Aiton (giant goldenrod)
Solidago missouriensis Nutt. (Missouri goldenrod) **MWP, L**
Solidago nana Nutt. (baby goldenrod) **FM**
Solidago nemoralis Aiton (gray goldenrod) **L**
Solidago velutina D.C. (three-nerve goldenrod)
Symphotrichum ericoides (L.) A. Löve & D. Löve (white heath aster) **MWP, L** as *Aster multiflorus*
Symphotrichum laeve (L.) A. Löve & D. Löve (smooth aster) **FM, MWP, L** as *Aster geyeri*
Symphotrichum lanceolatum (Willd.) G.L. Nesom (white panicle aster)
[*Thelesperma megapotamicum* (Spreng.) Kuntze (Hopi tea greenthread) **L** as *Thelesperma gracile*]
Tragopogon dubius Scop. (yellow salsify)
Tripleurospermum perforatum (Merat) M. Lainz (scentless false marigold) **FM**
Tetraneuris acaulis (Pursh) Greene (stemless four-nerve daisy)

Boraginaceae
Cryptantha cinerea (Greene) Cronquist {*Oreocarya suffruticosa*} (James' cryptantha) **X** [*Lappula occidentalis* (S. Watson) Greene (flatspine stickweed) **L**]
Mertensia lanceolata (Pursh) D.C. (prairie bluebells)
Onosmodium bejariense DC var. *occidentale* (Mack.) B.L. Turner {*Onosmodium molle* ssp. *occidentale*} (softhair marbleseed)
Plagiobothrys scouleri I.M. Johnst. (Scouler's popcorn flower)

Brassicaceae
Arabis holboelii Hornem. var. *retrofracta* Rydb. {*Boechera retrofracta*} (second rockcress) **FM**
Barbarea orthoceras Ledeb. (American yellowrocket)
Draba nemorosa L. (woodland draba) **FM**
Sisymbrium loeselii L. (small tumbleweed mustard)

Cactaceae
Pediocactus simpsonii (Engelm.) Britton & Rose (mountain ball cactus) **FM**
Opuntia polyacantha Haworth (plains prickly pear) **L**

Campanulaceae
Campanula rotundifolia L. (bluebell bellflower) **FM**
Lobelia siphilitica L. (great blue lobelia) **U, MWP, L** Common on the study site; regionally uncommon species

Caprifoliaceae
Symphoricarpos occidentalis Hook. (western snowberry)

Caryophyllaceae
Arenaria hookeri Nutt. {*Eremogone hookeri*} (Hooker's sandwort)
Stellaria longifolia Muhl. ex. Willd. (longleaf starwort) **FM**
Paronychia jamesii Torr. & A. Gray (James' nailwort) **X**
[*Silene scouleri* Hook. (simple campion) **L**] Species common in the foothills/montane zone but not currently known from this location

Chenopodiaceae (APG Amaranthaceae)
Chenopodium graveololens Willd. {*Teloxis graveolens*} (fetid goosefoot)
Chenopodium leptophyllum (Moq.) Nutt. (narrowleaf goosefoot), **L**
Cycloloma atriplicifolium (Spreng.) J.M. Coulter (winged pigweed)
Suaeda calceoliformis (Hook.) Moq. {Suaeda depressa} (Pursh seepweed)

Clusiaceae
Hypericum scouleri Hook. {Hypericaceae: *Hypericum formosum*} (Scouler's St. Johnswort) **FM**

Commelinaceae
Tradescantia occidentalis (Britton) Smythe (prairie spiderwort)

Crassulaceae
Sedum lanceolatum Torr. (spearleaf stonecrop)

Cyperaceae
Carex aurea Nutt. (golden sedge) **FM, U, L**
Carex brevior (Dewey) Mack. (shortbeak sedge) **L**
Carex crawei (Dewey) (Crawe's sedge) **R (S1), FM**
Carex disperma Dewey (softleaf sedge) **FM**
Carex douglasii Boot (Douglas' sedge)
Carex echinata Murray {*Carex angustior*}(star sedge) **FM, U**
[*Carex filifolia* Nutt. (threadleaf sedge) **L**]
[*Carex heliophila Mack.* = *C. inops* L.H. Bailey ssp. *heliophila* (Mack.) Crins (sunsedge) **L**]
[**Carex oreocharis* T. Holm (grassyslope sedge) **L**- not observed this study]
Carex pellita Muhl. {*Carex lanuginosa*} wooly sedge
Carex nebrascensis Dewey (Nebraska sedge) **L**
[**Carex hallii* Olney [*C. parryana* Dewey ssp. *hallii* [specimen coll. *R.B. Livingston 1430*: @COCO;] (deer sedge)]
[**Carex praegracilis* W. Boott) **L**-not observed this study]
Carex simulata Mack. (analogue sedge)
Carex xerantica L.H. Bailey (whitescale sedge)
Eleocharis acicularis (L.) Roemer & Schultes (needle spikerush)
Eleocharis obtusata (Willd.) Schult. (blunt spikerush)
[*Eleocharis palustris* (L.) Roem. & Schult. (common spikerush) **L**]
Eleocharis quinqueflora (Hartmann) O. Schwartz (fewflower spikerush) **FM**
Cyperus schweinitzii Torr. (Schweinitz' flatsedge) {*Mariscus schweinitzii*}
Schoenoplectus acutus (Muhl.) A. Löve & D. Löve {*Scirpus acutus*} (hardstem bulrush)
Schoenoplectus pungens (Vahl) Palla (common threesquare)
Schoenoplectus tabernaemontani (C.C. Gmelin) Palla (softstem bulrush) {*Scirpus lacustris*}
Scirpus microcarpus Presl. & C. Presl (panicled bulrush)

Equisetaceae
Equisetum arvense L. (field horsetail) **MWP, L**
Equisetum laevigata A. Brown (smooth horsetail) **MWP**

Euphorbiaceae
Chamaesyce glyptosperma (Engelm.) Small (ribseed sandmat) **L** as Euphorbia glyptosperma
Euphorbia brachycera Engelm. (horned spurge) **X**

Fabaceae
Amorpha fruticosa L. var. *angustifolia* Pursh (false indigo bush)
Astragalus canadensis L. (Canadian milkvetch) **U, MWP**
Dalea candida Michx. ex Willd. (white prairieclover) **MWP**
Dalea purpurea Vent. (purple prairieclover) **MWP, L** as *Petalostemon purpureus*
Gleditsia triacanthos L. (honeylocust) A single tree occurring on edge of study site near old ranch buildings.
Glycyrrhiza lepidota Pursh (American licorice) **MWP, L**
Lathyrus polymorphus Nutt. (manystem pea)
Lupinus pusillus Pursh (rusty lupine)
[*Melilotus officinalis* (L.) Lam. (sweetclover) **L** as *M. alba*]
Oxytropis multiceps Nutt. (Nuttall's oxytrope)
Robinia neomexicana A. Gray (New Mexico locust) Occasional trees occurring on edges of study site near old ranch buildings.
[*Thermopsis montana* Nutt. (mountain goldenbanner) **L**]
[*Trifolium pratense* L. (red clover) **L**]
[*Trifolium repens* L. (white clover) **L**]
[*Vicia americana* Muhl. ex Willd. (American vetch) **L**]

Gentianaceae
[*Gentiana affinis* Griseb. (pleated gentian) **L**]
Gentianella amarella (L.) Borner ssp. *acuta* (Michx.) Gillette {*Gentianella strictiflora*} (autumn dwarf gentian) **FM, L** As noted by Weber and Wittmann (2012), the densely white flowered form with a stiffly erect inflorescence is very distinctive in this region in the montane zone and in higher elevations on the plains; it is easily recognized as separate from the *amarella/acuta* form. The form occurring in the Black Squirrel Creek region is the "strictiflora" form, rather than the purple flowered, smaller "acuta" form.
Gentianopsis virgata (Raf.) Holub {*Gentianopsis procera* ssp. *crinita; G. crinita*} [lesser fringed gentian] **R (CHNP-Not rated), MWP** This species, recently confirmed by Flora of North America experts in the genus, is only known to occur in the upper Black Squirrel Creek drainage. Although not yet listed by Colorado Natural Heritage Program, its state rarity and disjunct connection to the Midwest prairie flora is notable.

Geraniaceae
Geranium atropurpureum A. Heller. {G. *caespitosum* ssp. *atropurpureum*}(western purple crane's bill) **FM**

Grossulariaceae
Ribes aureum Pursh (golden currant)

Haloragaceae
Myriophyllum sibiricum Kom. (shortspike watermilfoil)

Hippuridaceae (APG Plantaginaceae)
Hippuris vulgaris L. (common mare's tail) **FM**

Hypoxidaceae
Hypoxis hirsuta (L.) Coville (common goldenstar) **R (S1), MWP**

Iridaceae
Iris missouriensis Nutt. (wild iris)
Sisyrinchium montanum Greene (strict blue eyed grass) **FM, L** as S. angustifolium

Juncaceae
Juncus alpinoarticulatus Chaix (northern green rush)
Juncus arcticus Willd. ssp. *littoralis* (Willd.) Hultén {*J. arcticus* ssp. *ater*} (mountain rush), **L** as *J. balticus*
Juncus brachycephalus (Engelm.)Buchenar (smallhead rush) **R(S1), MWP,** L
Juncus brevicaudatus* (Engelm.) Fernald: narrowpanicle rush **R (S1); MWP A specimen of this species under the name *J. brachycephalus* (*Penland 4935*; COCO; OSH) was collected by in the Black Squirrel Creek drainage) and later verified by N. Harriman and F. Herrmann (Herrmann, 1975) as the very similar *J. brevicaudatus*. We have tentatively identified one of our collections as this species. It grows intermixed with *J. brachycephalus*.
Juncus bufonius L (toad rush)
Juncus dudleyi Wieg. (Dudley's rush)
Juncus interior Wieg. (inland rush)
Juncus longistylis Torr. (longstyle rush) **L**
Juncus marginatus Rostk. (grassleaf rush)
Juncus nodosus L. (knotted rush)
Juncus saximontanus A. Nelson (Rocky Mountain rush)
Juncus torreyi Coville (Torrey's rush) **L**

Juncaginaceae
Triglochin maritima L. (seaside arrowgrass) **L**
Triglochin palustris L. (marsh arrowgrass) **FM**

Lamiaceae
Lycopus americanus Muhl. ex Bartram (American water horehound) **MWP**
Mentha arvensis L. (wild mint)
Monarda fistulosa L. (wild bergamot) **MWP**
Prunella vulgaris L. (common selfheal) **L**
Scutellaria galericulata L. (marsh skullcap) **U**
Stachys palustris L. (marsh hedgenettle)

Lemnaceae
Lemna minor L. (common duckweed)

Lentibulariaceae
Utricularia minor L. **R(S2), FM**

Liliaceae s.l. (APG Amaryllidaceae)
Allium cernuum Roth (nodding onion) [Alliaceae] **L**
Calochortus gunnisonnii S. Watson (Gunnison's sego lily)
Lilium philadelphicum L. (wood lily) **R(S1), FM, MWP**

Lythraceae
Lythrum salicaria L. (purple loosestrife) This A list noxious weed has invaded a subsidiary drainage of Black Squirrel Creek, and is the only significant weed issue. It currently is not a monoculture, and many of the rare and unusual species are intermixed with it, making chemical controls problematic.

Malvaceae
Sidalcea neomexicana A. Gray (saltspring checkerbloom) **U, FM**

Najadaceae (APG Hydrocharitaceae)
Najas guadalupensis (Spreng.)Magnus (spring water nymph)

Nyctaginaceae
Abronia fragrans Nutt. ex Hook. (snowball sand verbena) **X**
Mirabilis linearis (Pursh)Heimerl {*Oxybaphus lanceolatus; Oxybaphus linearis*}(narrowleaf four o'clock)

Oleaceae
Forestiera pubescens Nutt. {*Forestiera neomexicana*} (stretchberry)

Onagraceae
Calylophus serrulatus (Nutt.) P. H. Raven (yellow sundrops)

Epilobium ciliatum Raf. ssp. *glandulosum* (Lehm.) Hoch & P. H. Raven (fringed willowherb)
Epilobium leptophyllum Raf. (bog willowherb)
Gaura coccinea Nutt. ex Pursh (scarlet beeblossom)
Gayophytum diffusum Torr. & A. Gray (spreading groundsmoke) **FM**
Oenothera coronopifolia Torr. & A. Gray (crownleaf evening primrose)
Oenothera flava (A. Nelson) Garrett (yellow evening primrose) **U**
Oenothera nuttallii Sweet (Nuttall's evening primrose)
Oenothera villosa Thunb. {*Oenothera strigosa*} (hairy evening primrose) **L** as *Anogra strigosa*

Orobanchaceae (s.str.)
Orobanche ludoviciana Nutt. (Lousiana broomrape) **X**

Oxalidaceae
Oxalis dillenii Jacq. (slender yellow wood sorrel)

Orchidaceae
Platanthera aquilonis Sheviak {*Limnorchis hyperborea, Platanthera hyperborea*} (northern green orchid) **FM**
Spiranthes romanzoffiana Cham. (hooded lady's tresses) **FM, U**

Plantaginaceae (s. str.; see also Scrophulariaceae s.l.)
Plantago elongata Pursh (prairie plantain)
Plantago patagonica Jacq. (woolly plantain) **L** as *P. purshii*)

Poaceae
Achnatherum nelsonii (Scribn.) Barkworth (Columbia needlegrass)
Agropyron cristatum (L.) Gaertn. (crested wheatgrass) **MWP**
Agrostis gigantea Roth. (redtop) **L** as *A. alba*
Agrostis scabra Willd. (rough bentgrass) **FM, L** as *A. hiemalis*
Alopecurus aequalis Sobol (shortawn foxtail) **FM**
Andropogon gerardii Vitman (big bluestem) **U, MWP, L** as *A. furcatus.* Generally occurring on the study site in dispersed patches; common but sporadic across plains and mesic drainages.
[*Andropogon hallii* Hack. **L**] Occurs sporadically in the area on deep sandy soils, but not present in our site.
Beckmannia syzigachne (Steud.) Fernald (American sloughgrass)
Bouteloua curtipendula (Michx.) Torr. (sideoats grama) **MWP**
Bouteloua gracilis (Willd. ex Kunth) Lag. ex. Griffiths {*Chondrosum gracile*} (blue grama) **L**
Bouteloua hirsuta Lag.) {*Chondrosum hirsutum*} (hairy grama)
Bromus carinatus Hook. & Arnott {*Ceratochloa carinata*} (California brome)
Bromus inermis Leyss. {*Bromopsis inermis*} (smooth brome)
Calamagrostis stricta (Timm.) Koeler (slimstem reedgrass) **FM**
Calamovilfa longifolia (Hook.) Scribn. (prairie sandreed) **MWP, L**
Hordeum jubatum L. {*Critesion jubatum*} (foxtail barley) **L**
Hordeum brachyantherum Nevski {*Critesion brachyantherum*} (meadow barley)
Distichlis spicata (L.) Greene (saltgrass) **L** Occurring with *Sporobolus airoides* along shallow alkaline drainages, lower portion of study site only and increasingly common to the south.
Elymus canadensis L. (Canada wildrye) **MWP**
Elymus lanceolatus (Scribn. & J.G. Sm.) Gould (thickspike wheatgrass)
Elymus trachycaulus (Link) Gould ex Shinners (slender wheatgrass) **L** as *Agropyron pauciflorum*
Glyceria striata (Lam.) Hitchc. (fowl mannagrass) **FM**
Hesperostipa comata (Trin. & Rupr.) Barkworth {*Stipa comata*} (needle and threadgrass) **X, L**
Hesperostipa spartea (Trin.) Barkworth {*Stipa spartea*} (porcupinegrass) **U, MWP, L**
[*Hordeum jubatum* L. (foxtail barley) **L**]
Koeleria macrantha (Ledeb.) Schult. (prairie junegrass) **MWP, L** as *K. cristata*
Muhlenbergia asperifolia (Nees & Meyer) Parodi (scratchgrass) **L**
Muhlenbergia minutissima (Steud.) Swallen (annual muhly)
Muhlenbergia montana (Nutt.) Hitchc. (mountain muhly) **FM**
Muhlenbergia richardsonis (Trin.) Rydb. **L** as *M. squarrosa*
Nassella viridula (Trin.) Barkworth {*Stipa viridula*} (green needlegrass)
Panicum virgatum L. (switchgrass) **MWP, L**
Pascopyrum smithii (Rydb.) Barkworth & D.R. Dewey {*Agropyron smithii, Elytrigia smithii*} (western wheatgrass **L**
Phleum pratense L. (timothy) **L**
Poa annua L. (annual bluegrass)
Poa fendleriana (Steud.) Vasey (muttongrass) **FM, L**
Poa leptocoma Trinius (marsh bluestem) **FM**
Poa nemoralis L. ssp. *interior* (Rydb.) W.A. Weber (inland bluegrass) **FM**
Poa pratensis L. (Kentucky bluegrass) **MWP, L**
Schizachyrium scoparium (Michx.) Nash (little bluestem) **MWP, L** as *Andropogon scoparius*
Sorghastrum nutans (L.) Nash (Indiangrass) **U, MWP, L**
Spartina pectinata Link (prairie cordgrass) **L**]
Sporobolus airoides (Torr.) Torr. (alkali sacaton)
[*Sporobolus cryptandrus* (Torrey) A. Gray (sand dropseed) **L**
Sporobolus heterolepis (A. Gray) A. Gray (prairie dropseed) **U, MWP, L**
Thinopyrum ponticum (Podp.) Z.W. Liu & R.C. Wang {*Elytrigia elongata*} (tall wheatgrass)

Polemoniaceae
Aliciella pinnatifida (Nutt. ex A. Gray) J.M. Porter (sticky gilia) **X, L** as *Gilia pinnatifida*
Collomia linearis Nutt. (tiny trumpet)

Polygonaceae
Eriogonum alatum Torr. {*Pterogonum alatum*} (winged buckwheat) **L**
Eriogonum annuum Nutt. (annual buckwheat) **L**
Polygonum amphibium L. {*Persicaria amphibian*} (water knotweed) **MWP**
Polygonum convolvulus L. {*Fallopia convolvulus*}(black bindweed)
Polygonum douglasii Greene (Douglas' knotweed)
Polygonum pensylvanicum L. (Pennsylvania knotweed)
Polygonum lapathifolium L. {*Persicaria lapathifolia*} (curlytop knotweed)
Polygonum punctatum Elliott {*Persicaria punctata*} (dotted knotweed)
Rumex crispus L. (curly dock)
Rumex acetocella L. {*Acetocella vulgaris*} (common sheep sorrel)

Portulacaceae
Phemeranthus calycinus (Engelm.) Kiger {*Talinum parviflorum*} (largeflower fameflower) **L**

Potamogetonaceae
Potamogeton natans L. (floating pondweed)
Potamogeton foliosus Raf. (leafy pondweed)

Primulaceae
Dodecatheon pulchellum (Raf.) Merr. (darkthroat shooting star) **FM**
Lysimachia ciliata L. (fringed loosestrife) **U, MWP**

Ranunculaceae
Anemone canadensis L. (Canadian anemone) **FM, MWP**
Anemone cylindrica A. Gray (candle anemone) **FM, MWP**
Myosurus minimus L. (tiny mousetail)
Ranunculus cardiophyllus Hook. (heartleaf buttercup) **FM**
Ranunculus trichophyllus Chaix (threadleaf crowfoot)

Rosaceae
Agrimonia striata Michx. (roadside agrimony) **U, FM**
Fragaria virginiana Miller (Virginia strawberry) **MWP**
Geum aleppicum Jacq. (yellow avens) **FM**
Potentilla arguta Pursh {*Drymocallis arguta*}(tall cinquefoil) **FM**
Potentilla hippiana Lehm. (woolly cinquefoil)

Potentilla norvegica L. (Norwegian cinquefoil)
Potentilla plattensis Nutt. (Platte River cinquefoil)
Prunus pumila L. var. *besseyi* (L.H. Bailey) Gleason {*Prunus besseyi*; *Cerasus pumila*} (western sandcherry)
Prunus virginiana L. {*Padus virginiana*} (chokecherry) **FM**
Rosa arkansana Porter (prairie rose) **MWP**

Rubiaceae
Galium boreale L. {*Galium septentrionale*} (northern bedstraw) **FM**
Galium trifidum L. (threepetal bedstraw) **M**F

Salicaceae
Populus × *acuminata* Rydb. (lanceleaf cottonwood)
Populus angustifolia James (narrowleaf cottonwood) **FM**
Populus deltoides Bartram ex Marsh. (plains cottonwood)
Salix amygdaloides Andersson (peachleaf willow)
Salix exigua Nutt. (narrowleaf willow)
Salix irrorata Andersson (deweystem willow) **FM**
Salix ligulifolia (C.R. Ball) C.R. Ball (strapleaf willow)

Santalaceae
Comandra umbellata (L.) Nutt. (bastard toadflax) **X, L** as *C. pallida*

Saxifragaceae
Parnassia palustris L. var. *parviflora* (DC) Boivin {*Parnassia parviflora*} (smallflower grass of Parnassus) **FM**

Selaginellaceae
Selaginella densa Rydb. (lesser spikemoss) **FM**

Scrophulariaceae (s. lat.; APG see also Callitrichaceae, Orobanchaceae, Phrymaceae)
Mimulus glabratus Kunth (roundleaf monkeyflower)
Nuttallanthus canadensis (L.) D.A. Sutton {*Linaria canadensis*} (Canada toadflax) **U**
Orthocarpus luteus Nutt. (yellow owlclover) **L**
Pedicularis canadensis L. (Canadian lousewort) **FM**
[*Penstemon angustifolius* Nutt. ex. Pursh (broadbeard beardtongue) **L**]
Penstemon auriberbis Pennell (Colorado beardtongue) **X** This species is extremely common south in the Arkansas River drainage but occurs only sporadically around Colorado Springs.
Penstemon glaber Pursh (sawsepal pentstemon) **FM**
Penstemon gracilis Nutt. (lilac penstemon)**U, FM, MWP** Species uncommon in the foothills and pine savannah regions of the Black Forest area; found once on our study site.
Penstemon virgatus ssp. *asa-grayi* Crosswhite (one-sided penstemon)
Veronica anagallis-aquatica L. (water speedwell) {*Veronica catenata*}
Veronica peregrina L. (neckweed) **L**
Veronica serpyllifolia L. ssp. *humifusa* (Dicks.) Syme (thymeleaf speedwell) **FM**

Solanaceae
Physalis virginiana Mill. (Virginia groundcherry)

Sparganiaceae (APG Typhaceae)
Sparganium angustifolium Michx. (narrowleaf bur-reed) **FM**

Typhaceae
Typha latifolia L. (broadleaf cattail)

Valerianaceae (APG Caprifoliaceae)
Valeriana edulis Nutt. ex Torr. & A. Gray (tobacco root) **FM**

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